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Feeding Opportunism of the Red Swamp Crayfish, *Procambarus clarkii*, an Invasive Species

Francesca Gherardi † and Silvia Barbaresi

Dipartimento di Biologia Evoluzionistica, Università di Firenze,
Via Romana 17, 50125 Firenze, Italy
† Corresponding Author — *E-mail: francesca.gherardi@unifi.it*

Abstract.— We analyzed the feeding behavior of the red swamp crayfish, *Procambarus clarkii*, by assessing the composition and quantity of the diet of invasive populations inhabiting three different aquatic systems in southern Europe. Gut content analyses showed that this species, regardless of sex, season, and site, consumes relatively large quantities of organic detritus and plants, particularly non-green portions of macrophytes. Conversely, animal remains found in the crayfish's guts (including terrestrial insects, mosquitofish, and conspecifics) were scarce as a confirmation of previous studies suggesting that the adults of this species are seldom zoophagous. The taxonomic composition of the ingested plants varied across sites and seasons in accordance with the diverse species dominating in each individual habitat. These results are clear in showing *P. clarkii*'s ability in adjusting its feeding behavior to the prey items available in the colonized habitats. [*Keywords*.— diet; feeding behavior; invasive crayfish; *Procambarus clarkii*; opportunism].

INTRODUCTION

Today, there is a wide consensus that the human-mediated introductions of species outside their native range work as powerful drivers of biodiversity change in inland waters (Sala et al. 2000; Gherardi 2007a). Acting in concert with climate change, habitat loss and fragmentation, overexploitation, and pollution, the spread of non-indigenous species often leads to irreversible modifications in the specific composition of aquatic communities (Gherardi 2007a, 2007c; Gherardi et al. 2008) and to the consequent drastic decrease in the pristine regional differences among ecosystems (i.e., biotic homogenization; Rahel 2000). At the currently recorded speed of homogenization, it has been said (Taugbøl and Skurdal 1999), in less than 100 years almost all European watersheds will be dominated by a handful of cosmopolitan species among mammals, fish, mussels, crayfish, and plants.

Among these taxa, crayfish have received by far the least attention from biologists, policy makers, and the general public (Lodge et al. 2000) despite the long history of introductions (Gherardi and Holdich 1999) on one hand, and their prominent role in freshwater ecosystems (Gherardi 2007b) on the other. Crayfish are the largest invertebrates in temperate areas, often occurring at high densities and acting as keystone species (Nyström et al. 1996). Additions of crayfish species have had significant consequences on the structure of freshwater food webs (Covich et al. 1999) since they affect all levels of ecological organization, from subtle behavioral modifications in resident species to altered energy and nutrient fluxes in the ecosystem (Gherardi 2007b).

At the community level, the impact of the introduced crayfish can be particularly strong when they experience little predation or competition from native predators and find prey that lack efficient defense adaptations to them (Nyström et al. 2001). Dramatic direct and indirect effects on ecosystems derive from the mode of resource acquisition by crayfish and from their capability to develop new trophic relationships (Gherardi 2007b). Most species are known to be polytrophic and opportunistic consumers, feeding on benthic invertebrates, detritus, macrophytes, and algae in both lotic and lentic waters (e.g., Whitledge and Rabeni 1997).

Aims of this study were to investigate the temporal and sexual correlates of food consumption in an emblematic invasive crayfish, *Procambarus clarkii* (Girard), and to compare the diet of populations of this species that have colonized three different aquatic systems (i.e., an artificial irrigation system, a natural lake, and a rice field). Most of the previous information concerning the feeding habits of *P. clarkii* refers to commercial ponds (e.g., D'Abramo and Robinson 1989) and laboratory experiments (e.g., Covich et al. 1981; Wiernicki 1984; Brown 1990; Ilhéu and Bernardo 1993a; Cronin et al. 2002; Alcorlo et al. 2004; Cirujano et al. 2004), whereas available data are relatively scarce for natural or semi-natural habitats (Feminella and Resh 1989; Ilhéu and Bernardo 1993b; Guitiérrez-Yurrita et al. 1998; Correia 2002, 2003; Anastácio et al. 2005a, 2005b; Correia et al. 2005). No previous studies have adopted a comparative approach, whereas this is obviously needed when the purpose is to understand the opportunism in the feeding behavior of a species, and thus to explain its role of energy transformer in the colonized systems (Guitiérrez-Yurrita et al. 1998).

METHODS

The Study Animal

Due to the high commercial value of crayfish, their introduction and cultivation in Europe have increased during the last few decades (e.g., Pérez et al. 1997). Today, most European countries

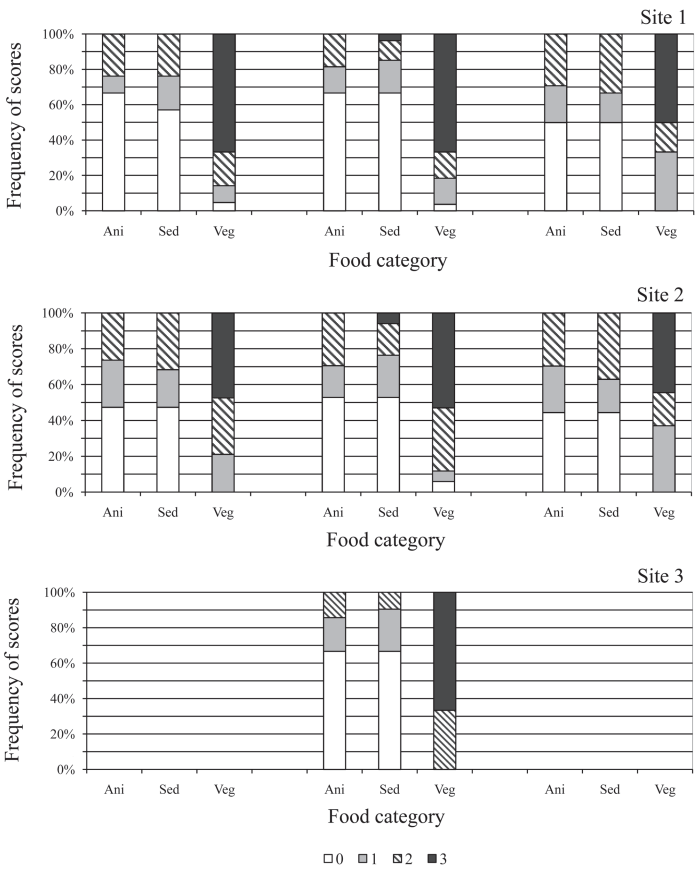

Figure 1. Frequency (in %) of the scores characterizing the relative volume in the crayfish guts of the three food categories; animal remains (Ani), inorganic sediments (Sed), and vegetal items (Veg), compared among sampling sites and seasons of collection. Scores ranged from a minimum of 0 (0 – 25% of volume) to a maximum of 3 (76 – 100% of volume).

have at least one non-indigenous crayfish species (Gherardi and Holdich 1999). Once imported for aquaculture and kept in outdoor ponds, crayfish almost inevitably escape (Hobbs et al. 1989), forming self-sustaining populations that often become dominant and spread to other waterbodies (Kolar and Lodge 2001; Gherardi 2006a).

Procambarus clarkii is an emblematic invasive species (Gherardi 2006b). From its natural range of distribution (i.e., north-eastern Mexico and south-central USA (Hobbs 1972)), this species has been introduced worldwide, with the exceptions of Australia and Antarctica (Huner and Avault 1979). The first introduction of *P. clarkii* into Spain in 1973 (e.g., Gutiérrez-Yurrita et al. 1999) was followed by its translocation into many other European countries, including Italy (Barbaresi and Gherardi 2000; Souty-Grosset et al. 2006), and by several sequential introductions from different donor areas, such as the Far East, as recently suggested by genetic studies (Barbaresi et al. 2003, 2007).

Sampling Sites

Three sampling sites were chosen as representatives of the different aquatic habitats invaded by *P. clarkii.* These included a ditch system in the neighborhood of Florence, Italy, composed of a network of canals, approximately 1.5 m wide, with 15 – 25 cm water depth (Gherardi et al. 2000; Barbaresi et al. 2004; site 1); the Massaciuccoli Lake, Italy, which is a shallow coastal and eutrophic lake with an average depth of 2 m and a surface area of 6.8 km^2 (Giulia et al. 2004; site 2), and a 8 km^2 rice field in the Lower Guadalquivir, Spain (Gherardi and Barbaresi 2000; site 3). Abundant populations of *P. clarkii* now inhabit these three sites after their introduction in the 1990s (sites 1 and 2) and the 1970s (site 3). At site 1, aquatic vegetation is dominated by the monocotyledons *Typha latifolia* Linnaeus (Typhaceae), *Sparganium erectum* Linnaeus (Sparganiaceae), and *Lemna* sp. (Araceae), while riparian vegetation consists mostly of *Urtica* sp. (Urticaceae), *Ranunculus* sp. (Ranunculaceea), and *Paspalum digitaria* Müll. Stutg. (Paniceae). In summer, drought was accompanied by a drastic reduction in the abundance of *T. latifolia*. At site 2, the monocotyledons *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) and *Cladium mariscus* (Linnaeus) Pohl. (Cyreraceae) are the most abundant macrophytes. At site 3, crayfish were sampled when the rice field was flooded and the crop (composed of *Oryza sativa* Linnaeus, Poaceae) was not yet harvested.

Sampling

Sampling at sites 1 and 2 was conducted in spring, summer, and autumn 2000 (winter was excluded because of the scarce crayfish activity recorded; Gherardi et al. 2002), and in summer (August) 1998 at site 3. To capture crayfish we used 50 cm long cylindrical traps, constructed with a 2 mm wire net with two opposing apertures of 23 cm in diameter. Between two and six traps were placed into the three sampling sites 50 – 100 m apart at dawn, when crayfish activity is highest (Gherardi et al. 2000). In order to avoid cannibalism by crayfish and to minimize their ingestion of other animals caught in the traps at the same time (e.g., fish, coleopterans, or branchiopods), traps were recovered and emptied every 1 h until midnight.

Immediately upon capture, crayfish were transported to the laboratory, where they were sexed and measured (cephalothorax length, including rostrum) with a vernier caliper. Samples from each site consisted of a total of 17 – 27 adult crayfish, composed of females (cephalothorax length: 32 – 62.3 mm) and Form I (= reproductive) males (cephalothorax length: 32.8 – 60.2 mm). Then, foreguts (hereafter called guts) of each crayfish were removed to interrupt digestion and to preserve the ingested material in a recognizable condition. Only the content of the foreguts were examined, since nearly all items in the mid- and hindguts were digested beyond recognition.

Qualitative and Quantitative Analyses of Gut Contents

Immediately upon removal, the fullness (in %) of each gut was estimated by sight. Then, following Gherardi et al. (2004), guts were split and their content was placed in a Petri dish with a small amount of water, distributed as evenly as possible, and viewed under a dissecting microscope (magnification 30x). First, we distinguished amorphous material (i.e., small organic detritus of plant origin in an advanced state of decay) from the remaining content. The latter was then classified into three food categories, either vegetal items, animal remains, and inorganic sediments and their relative volume, excluding amorphous material, was estimated by sight, assigning each of them to one of four scores,

Table 1. Mean and standard error (SE) of some quantitative parameters of *Procambarus clarkii*'s gut contents compared between sexes for each season and sampling site (Student's t-test after arcsine square root transformation for percentages).

Site 1	**Males**			**Females**			**Males vs Females**	
spring	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	68.2	7.6	11	77.5	6.9	10	0.826	19
dry weight (mg)	53.4	7.6	11	73.6	12.2	10	1.455	19
organic C (%)	31.5	1.4	11	28.3	1.6	10	1.523	19
organic N (%)	2.6	0.1	11	2.6	0.2	10	0.083	19
C:N	11.9	9.8	11	10.8	6.5	10	1.324	19
summer	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	76.5	6.2	17	77.5	8.7	10	0.216	25
dry weight (mg)	64.1	12.7	17	86.8	19.9	10	1.011	25
organic C (%)	33.7	1.6	17	34.1	1.0	10	0.218	25
organic N (%)	4.2	0.3	17	5.1	0.4	10	2.007	25
C:N	8.2	5.9	17	6.9	3.0	10	1.903	25
autumn	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	64.6	9.5	12	81.3	7.6	12	1.219	22
dry weight (mg)	61.6	11.5	12	85.8	18.3	12	2.037	22
organic C (%)	37.6	0.7	12	38.5	1.1	12	0.594	22
organic N (%)	4.2	0.3	12	3.8	0.2	12	0.948	22
C:N	9.2	2.3	12	10.2	5.8	12	1.034	22
Site 2	**Males**			**Females**			**Males vs Females**	
spring	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	50.0	9.1	10	55.6	9.1	9	0.201	17
summer	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	65.6	8.1	8	75.0	7.2	9	0.959	15
autumn	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	71.2	6.8	13	60.7	6.8	14	1.126	25
Site 3	**Males**			**Females**			**Males vs Females**	
summer	mean	SE	n	mean	SE	n	t	df
gut fullness (%)	72.5	6.8	10	65.9	6.4	11	0.569	19

from 0 (0 – 25%) to 3 (76 – 100%). A finer analysis was also made by distinguishing vegetal items into monocotyledons, dicotyledons, green algae, and seeds, and, when possible, down to the species level. Animal remains were classified as insects, adults (mostly ants, Dytiscidae, and Gerridae) or aquatic larvae (such as Chironomidae and Culicidae), crayfish (recognizable from pieces of their exoskeleton), and fish (*Gambusia* sp.).

Individual gut contents of the crayfish collected at site 1 were frozen to allow for a subsequent quantitative study. These samples were dried for two days in an oven at 80°C and weighed using an electronic balance. Finally, the percentages of organic carbon and nitrogen contents were evaluated using a gas-chromatography technique (Carlo Erba NA 1500 Analyser).

Statistical Analyses

Data were first tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variance using the Levene test. Student's t-tests (statistic: t) and one-way ANOVAs (after arcsine square root transformation for percentages; statistic: F) were used to compare gut content variables between sexes and among seasons, respectively (Zar 1999). When significant differences were found after one-way ANOVAs, pairwise comparisons were made with *post hoc* Tukey tests. Frequency data were analyzed

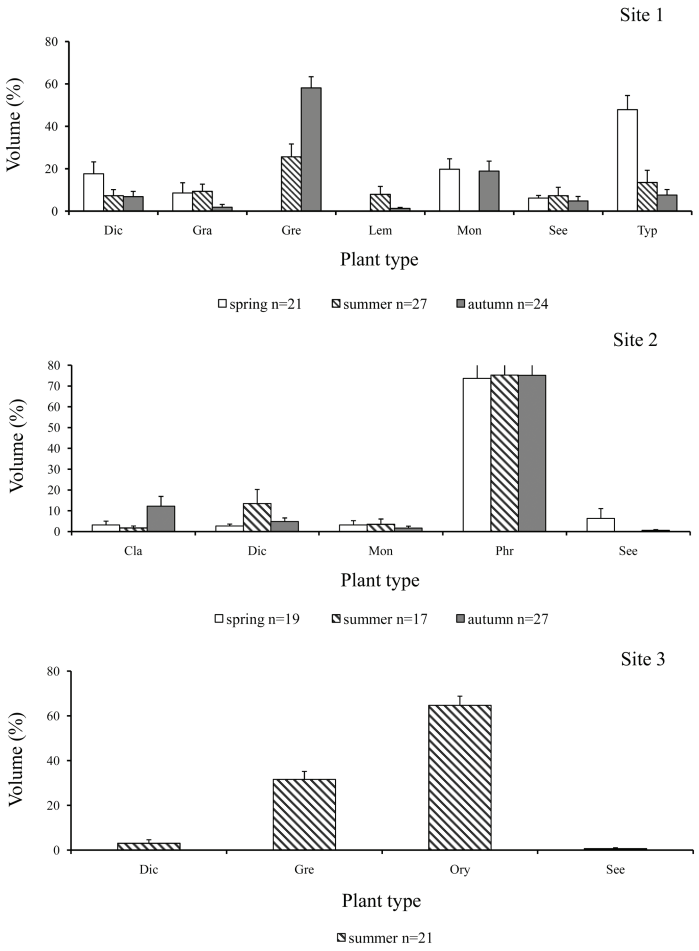

Figure 2. Volume (in %) of different plant types found in crayfish guts compared among sampling sites and seasons of collection. Abbreviations mean: Cla = *Cladium mariscus*; Dic = undetermined dicotyledons; Gra = Graminaceae; Gre = undetermined green algae; Lem = *Lemna* sp.; Mon = undetermined monocotyledons; Ory = *Oryza sativa*; Phr = *Phragmites australis*; See = Seeds; Typ = *Typha latifolia*.

using Wilks test (statistic: G) after Williams' correction. The level of significance at which the null hypothesis was rejected is $\alpha = 0.05$.

RESULTS

Amorphous Material

On average, 30% of the gut volume was composed of amorphous material at site 1 independently of sexes (spring: t = 0.063, df = 19; summer: t = 0.327, df = 25; autumn: t = 0.706, df = 22; *P* always > 0.05) and seasons (F = 3.25, df = 2, 69, *P* > 0.05). At site 2, a significant difference was found among seasons, the ingested amorphous material being more voluminous in spring than in summer or autumn (65% vs. 43% and 40%, F = 3.7, df = 2, 60, *P* < 0.05, after Tukey test), but not between sexes (spring: t = 0.886, df = 17; summer: t = 0.827, df = 15; autumn: t = 0.725, df = 25; *P* always > 0.05). At site 3, its amount reached 29% of volume in both sexes (t = 1.544, df = 19, *P* > 0.05). A comparison among sites on the data pooled among sexes showed that amorphous material was more abundant in summer (F = 14.08, df = 2, 62, *P* < 0.001, after Tukey test) at site 2 (65%) than at sites 1 (28%) and 3 (27%).

Vegetal Items

Since the ingested amount of all food categories did not differ between sexes (after G tests for scores and Student's t test for relative volumes, *P* always > 0.05), the analyses that follow were made on pooled data.

The guts that contained a relatively larger fraction of vegetal items (scores 2 and 3) were always significantly more numerous than those that scored high for the other food categories (site 1, spring: G = 43.911, df = 6, *P* < 0.001; summer: G = 54.764, df = 6, *P* < 0.001; autumn: G = 46.473, df = 6, *P* < 0.001; site 2, spring: G = 32.580, df = 6, *P* < 0.001; summer: G = 25.599, df = 6, *P* < 0.001; autumn: G = 47.159, df = 6, *P* < 0.001; site 3, summer: G = 60.379, df = 6, *P* < 0.001) (Figure 1). No difference either among seasons (site 1: G = 5.330, df = 6, *P* > 0.05; site 2: G = 7.252, df = 6, *P* > 0.05) or, in summer, among sites (G = 7.820, df = 6, *P* > 0.05) was found for their frequency distributions.

The most frequent plants contained in crayfish guts were *Typha* in spring (F = 8.329, df = 4, 100, *P* < 0.0001) and undetermined green algae in summer and autumn at site 1 (summer: F = 37.270, df = 6, 182, *P* < 0.0001; autumn: F = 2.485, df = 5, 138, *P* < 0.0001), *Phragmites* in each season at site 2 (spring: F = 44.678, df = 4, 90, *P* < 0.0001; summer: F = 34.882, df = 3, 64, *P* < 0.0001; autumn: F = 63.891, df = 4, 130, *P* < 0.0001), and *Oryza* at site 3 (F = 105.211, df = 3, 80, *P* < 0.0001) (Figure 2). Overall non-green plant material (at site 1: seeds and non-green fragments of Graminaceae, *T. latifolia*, and other undetermined monocotyledons; at site 2: non-green fragments of *C. mariscus* and *P. australis*) were more abundant than green ones (t always > 3.551, df between 40 and 52, *P* always < 0.001) except in summer at sites 1 and 3 (green plants > non-green plants: t = 4.031, df = 52, *P* < 0.001 and t = 33.498, df = 40, *P* < 0.0001) and in autumn at site 1 (non-green plants = green plants: t = 0.936, df = 46, *P* > 0.05).

Animal Remains

Because of the low occurrence of animal remains, data were pooled among seasons. At site 1, adult insects were more abundant than the other animal prey (G = 16.729, df = 3, *P* < 0.001) (Figure 3). At site 2, crayfish were the most represented category (G = 8.486, df = 3, *P* < 0.05), whereas at site 3 animal fragments belonged exclusively to adult insects (Figure 3).

Gut Fullness, Dry Weight, Organic Content, and C:N

Gut fullness for each site, dry weight, organic content of guts, and C:N from site 1 are shown in Table 1. No difference was ever found for gut fullness either among seasons in sites 1 (F = 0.32, df = 2, 67, *P* > 0.05) and 2 (F = 2.93, df = 2, 60, *P* > 0.05) or between sexes per season (Table 1). Neither did we find any difference among sites in summer (F = 0.57, df = 2, 62, *P* > 0.05).

At site 1, gut contents showed a similar dry weight and C:N when seasons (F = 0.29, df = 2, 67, *P* > 0.05; F = 1.15, df = 2,67, *P* > 0.05) and sexes were compared (Table 1). Conversely, organic carbon content was significantly higher in autumn than in summer and spring (F = 15.96, df = 2, 66, *P* < 0.01; after Tukey test) (Table 1) and organic nitrogen was higher in summer and autumn than in spring (F = 31.38, df = 2, 66, *P* < 0.01, after Tukey test).

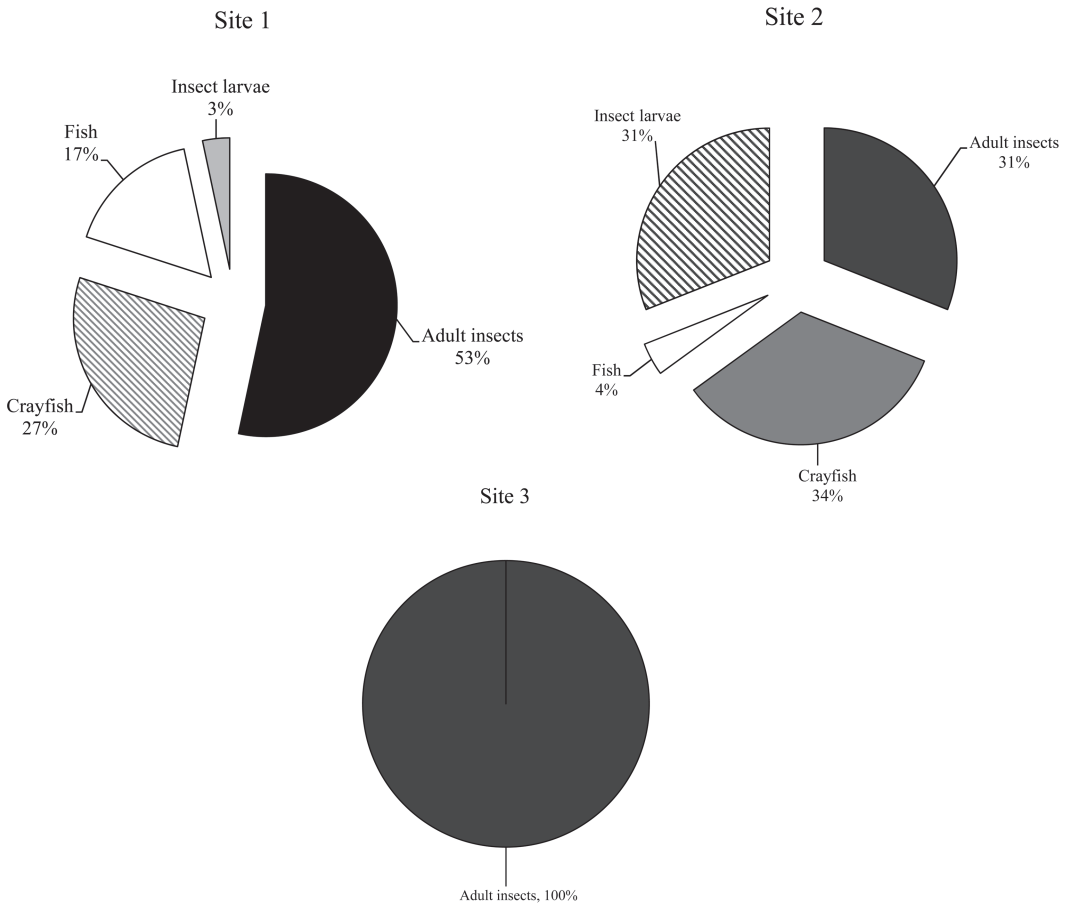

Figure 3. Volume (in %) of the remains of different animal prey found in crayfish guts compared among sampling sites.

DISCUSSION

Our comparative study confirms the often claimed (but seldom demonstrated) opportunism in the feeding habits of the red swamp crayfish, *P. clarkii* (Gherardi and Holdich 1999; Gherardi 2006b). Gut content analyses, in fact, showed that this species feeds on the more abundant items available in a given colonized habitat and that the composition of the diet, but not its quantity (as revealed by the constant gut fullness and weight), changes with sites and seasons according to the occurrence of the diverse food items.

A drawback of our study is to have limited the analysis to gut contents. The information obtained through this method, in fact, may be biased due to the different digestion rate of the diverse food items (Crehuet et al. 2007).

Whereas soft items are assimilated easily and rapidly, others (or their hard parts) can remain longer in crayfish guts, thus increasing their probability of being found and recorded (Correia 2003). More refined methods, such as the use of stable isotopes, are certainly more accurate in identifying the main energy sources in the long term (Bondar et al. 2005) but are obviously more expensive and cannot identify the taxonomic composition of the diet. Besides, when the purpose of the study is mainly comparative, gut content analysis offers a reliable aid to the understanding of diversities/similarities between sexes and among sites and seasons, providing some interesting results as follows.

Firstly, our study failed in finding any sex-related difference in either the composition of gut contents or the amount of the ingested material, which was, on the contrary, expected particularly in autumn, immediately following the reproductive season. Since females are less active than males during the breeding period (e.g., Gherardi et al. 2000), it is reasonable to expect that also their diet, along with gut fullness and weight, should differ from the other sex. Effects of gender were previously reported by Capelli (1980) in *Orconectes propinquus* (Girard) and by Guitiérrez-Yurrita et al. (1998) and Correia (2003) in two populations of *P. clarkii* inhabiting a temporary marsh in Spain and a rice field in Portugal, respectively. Taken together, these studies might suggest that females, after having released their offspring (L. Aquiloni and F. Gherardi, personal observations), increase their feeding rate to compensate for the inactivity displayed during their brooding for juveniles (E. Tricarico, personal observation).

A second result of our study is to have recorded a nearly constant proportion of the diverse food categories occurring in the crayfish guts regardless of the site. A large portion (30 – 65%) of crayfish guts, with a slight variation across seasons, was composed of detritus of plant origin (visualized here as amorphous material), suggesting that its consumption by *P. clarkii*, regardless of the habitat, can be intense throughout the whole year (Ilhéu and Bernardo 1993a; Correia 2003; Alcorlo et al. 2004). Indeed, detritus may be a highly nutritive food for crayfish because of its "microbial

conditioning" or "chemical-defense leaching" (e.g., Newman 1991); it is easily handled by crayfish (Cronin et al. 2002), being even preferred to green plants in laboratory experiments (Ilhéu and Bernardo 1995). Besides, assimilation efficiency seems to be higher when *P. clarkii* feeds on 15-day old detritus if compared to fresh pieces of macrophytes (Ilhéu and Bernardo 1995) and young-of-the-year of this species are able to survive when fed decaying vegetation alone (McClain et al. 1992).

The by far larger part of the remaining gut content was composed, regardless of the season, of fresh plants, whereas animal remains and inorganic sediments accounted for a relatively small portion of it. This result supports the claim that *P. clarkii* is mainly an herbivorous species (Penn 1943; Avault et al. 1981; Feminella and Resh 1989) and confirms data from a previous mesocosm study that quantified its intense grazing on macrophytes (Gherardi and Acquistapace 2007). However, although several authors have described *P. clarkii* to feed mainly on green parts of plants (e.g., Avault et al. 1981; Feminella and Resh 1989), the consumption of non-green plant material seemed, with a few exceptions, to be substantial in the habitats studied here. Changes across sites in the taxonomic composition of plants provide clear evidence of *P. clarkii*'s opportunism, the plant species that dominated in each habitat type were also the more highly represented in the crayfish guts (i.e., *T. latifolia* in Osmannoro, *P. australis* in Massaciuccoli Lake, and obviously *O. sativa* in the rice field). Similarly, a reversal in the dominance of vegetal species, as recorded with the progressive desiccation of ditches at site 1, seemed to induce a shift from a diet based on *Phragmites* in spring to one based on green algae in the subsequent seasons.

Consumption of animals was always much lower than that of detritus and plants, notwithstanding that it is possibly subject to a significant change across seasons, crayfish ingesting relatively more abundant animal protein in summer and autumn than in spring (but C:N remained constant across seasons). The scarcity of animal remains found in *P. clarkii*'s guts may be the effect of our underestimation of crayfish preference for animal prey (Whitledge and Rabeni 1997); indeed, cultivated *P. clarkii* of all ages and sizes show a quick response to fresh animal material and growth rates are greatly enhanced when animal protein are provided (Huner 1994, 2002). Alternatively, our result may confirm previous evidence that zoophagy is limited in this species (e.g., Gutiérrez-Yurrita et al. 1998), notwithstanding *P. clarkii*'s ability to prey upon several macroinvertebrates, particularly mollusks, and vertebrates, including amphibian larvae (Gherardi et al. 2001; Renai and Gherardi 2004). When abundant in the habitat, such as in a rice field of Portugal, aquatic macroinvertebrates can be easily consumed by *P. clarkii*, but their exploitation seemed to be proportional to, or even lower than their availability (Correia 2002, 2003). Conversely, juveniles are known to be more carnivorous than the adults, gradually shifting towards a more vegetarian diet with growth (Momot et al. 1978; Ilhéu and Bernardo 1993a; Momot 1995; Correia 2003).

The data collected here have the merit to expand the previously compiled list of *P. clarkii*'s animal prey (Correia 2003) with the inclusion of terrestrial insects, such as ants, as a confirmation of its amphibious behavior (Gherardi and Barbaresi 2000). Mosquitofish can be also occasionally ingested, as shown in a laboratory experiment by Gherardi et al. (2001) and in field studies by Gutiérrez-Yurrita et al. (1998), Correia (2002, 2003), and Leite et al. (2005), but the effective direct impact on this and other motile species has been recently questioned (Gherardi and Acquistapace 2007). Apart from ideal conditions in very small temporary pools (Ilhéu et al. 2007), *P. clarkii* was most often found to feed on dead, dying or immobilized fish (Lowery and Mendes 1977; Renai and Gherardi 2004) and on their eggs (Xinya 1995). Finally, crayfish remains in gut contents, particularly abundant in sites 1 and 2, are symptomatic of *P. clarkii*'s cannibalistic habit, which provides supplementary food requirements critical for growth, such as calcium (Lorman and Magnuson 1978).

To conclude, notwithstanding the difficulties usually encountered in collecting data on the trophic ecology of a species and the biases of the method adopted here, our comparative results are clear in showing the ability of *P. clarkii* in adjusting its feeding behavior to the availability of the prey items found in the colonized habitats. Feeding opportunism is a prerequisite for the rapid increase in the population density of this species, its rapid acquisition of a dominant position over the community, and the subsequent expansion of its range to new areas, all properties that make *P. clarkii* a successful invader (Gherardi and Holdich 1999; Gherardi 2006b; Gherardi 2007b).

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